principles of organization and development which have permitted biologists to better understand woody plants in both tropical and temperate regions.

However, the form of an adult tree is not only the result of the plan of its architectural model. Variation in form usually occurs within any one model by the process of reiteration (DE CASTRO E SANTOS, 1980) in which the pattern of the young tree, the idealized hereditary model, repeats itself within an individual. In addition, there is variation in the ability of different species showing the same model to undergo later changes in crown geometry, previously termed their degree of architectural plasticity, which seems to be related to ecological or adaptive differences (FISHER & HIBBS, 1982). There are also some examples of one species displaying a rarely occurring or genetically induced change in the typical architectural model for that species (HALLÉ, 1978). Some trees display growth patterns that are difficult to place into a particular model, e.g. the problem of leader formation in *Tsuga* (HIBBS, 1981) or the distal plagiotropy of old lateral branches in *Rhizophora* (HALLÉ et al., 1978).

In this report, we describe the architecture of a small tropical tree which shows characteristics of both Prévost's and Koriba's models (HALLÉ et al., 1978) in the way leader axes are initiated. In fact, it is difficult to distinguish the basic model from its reiteration. Such architectural plasticity may be an important feature in the biology of this species. We describe in quantitative terms the change in branching angles and branch geometry that result in a shift from radial to dorsiventral symmetry. In addition, we use these parameters of branch geometry in computer simulations and analyses of tree architecture which expand upon previous simulations of other models (HONDA et al., 1981, 1982 ; FISHER & HONDA, 1977 ; DE REFFYE, 1983).

## MATERIALS AND METHODS

Seeds of *Neea amplifolia* Donn. were collected along the Caribbean Sea coast at Punto Cahuita (south of Limón), Costa Rica. Plants were cultivated in Miami, Florida in large containers and were grown under partial shade (50-60 % full sun). Observations and measurements of the same trees were made over a period four years. Angles were measured directly on trees or camera lucida drawings of sectioned apical buds ; inclination was measured with a weighted protractor.

Developmental stages of apices from seedlings and branches were fixed in FAA (formalin, alcohol, acetic acid), imbedded in paraffin, serially sectioned at 10 μm, and stained with safranin and chlorazol black E.

Simulations were carried out on a UNIVAC computer using a Fortran program and drawn on a Hewlett-Packard plotter.

## OBSERVATIONS

SEEDLING

Germination is epigeal ; there are two, opposite, reniform cotyledons. The orthotropic axis bears alternate, oblanceolate leaves in an approximately 3/8 or possibly 2/5 phyllotaxy (Pl. 1, *E*). Most leaves subtend two serial buds of which the upper or distal bud is

larger. The original seedling axis terminates in an inflorescence (or rarely a parenchymatization of the apical meristem) when it is 0.5-1.0 m tall. There is a terminal cluster of usuaily three, sometimes four, leaves which follow the foliar helix but are separated by short internodes (Pl. 1, *F*).
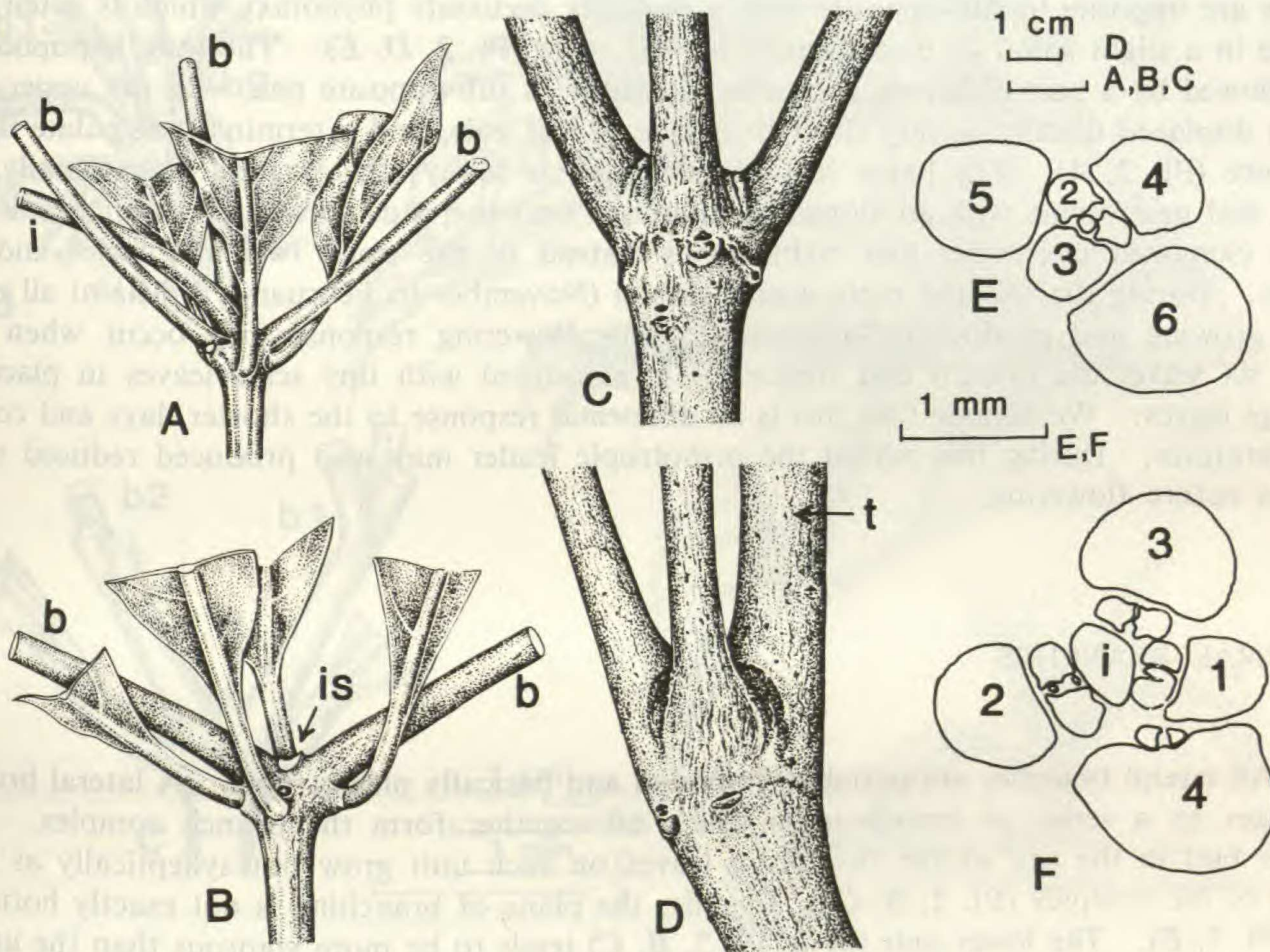
Pl. 1. — **Neea amplifolia** : **A**, first branching of sapling, terminal inflorescence (i) and three branches (b) ; **B**, first branching of sapling, terminal inflorescence scar (is) and two branches (b) ; **C**, point of first branching in older plant with three branches as in A ; **D**, point of first branching in older plant with two branches as in B but with a new trunk unit (t) from a proleptic bud ; **E**, apical bud of sapling before terminal inflorescence is present, leaves numbered in sequence in this transverse section ; **F**, apical bud of sapling after inflorescence (i) and sylleptic branch buds are present, leaves numbered in sequence in this transverse section. Scale lines indicate magnification.

Three (in 70 % of 10 observed saplings) or two (in 30 %) axillary buds grow out as sylleptic branches (Pl. 1, *A-D*). These first branches arise from the larger distal bud in each leaf axil and show typical sylleptic morphology (HALLÉ et al., 1978) : an elongated basal internode (= hypopodium), no basal scalelike prophylls, and foliage leaves as the first foliar organs on the branch.

## MODULE OR BRANCH UNIT

The branches are determinate morphological units or modules (= "articles"). The leaves are opposite to sub-opposite with a basically decussate phyllotaxy which is often distorted in a slight spiral or displacement of leaf pairs (Pl. 2, *D, E*). The long hypopodium is followed by a pair of leaves, a shorter internode, a sub-opposite pair with the upper leaf often displaced distally, a very short internode, a leaf pair, and a terminal paniculate inflorescence (Pl. 2, *A*). The lower leaf of each pair is always the larger. Occasionally, an extra leaf pair occurs with an elongated internode on either side so that the branch unit has three elongated internodes and eight leaves instead of the usual two internodes and six leaves. During the fall and early winter season (November to February) in Miami all units stop growing and produce inflorescences. This flowering response may occur when less than six leaves are present and frequently is associated with tiny scale leaves in place of foliage leaves. We assume that this is an abnormal response to the shorter days and cooler temperatures. During this period the orthotropic leader may also produced reduced scale leaves before flowering.

## LATERAL BRANCHES

All lateral branches are initially sympodial and basically plagiotropic. A lateral branch enlarges by a series of branch units which all together form the branch complex. The upper bud in the axil of the two distal leaves on each unit grow out sylleptically as new units of the complex (Pl. 2, *B, C*). Usually, the plane of branching is not exactly horizontal (Pl. 2, *E*). The lower unit (b1 in Pl. 2, *B, C*) tends to be more vigorous than the upper (b2) and has larger leaves and longer internodes. Therefore, ramification within a branch complex is asymmetrical, and one or more main lateral branch axes are established by a series of lower units (b in Pl. 4, *A*) by a process described in the section on geometry. Lateral branches grow and flower continuously except for the cooler months (November to February) in Miami. Plants were only observed in their native habitat during the month of May.

## TRUNK FORMATION

The original seedling axis establishes the base of the orthotropic trunk, and it ends in a tier of lateral branch complexes (Pl. 1, *A, B*; 3, *A, C*). A trunk is built up by a later series of orthotropic, sympodial units which can develop in two different ways, either proleptically or sylleptically.
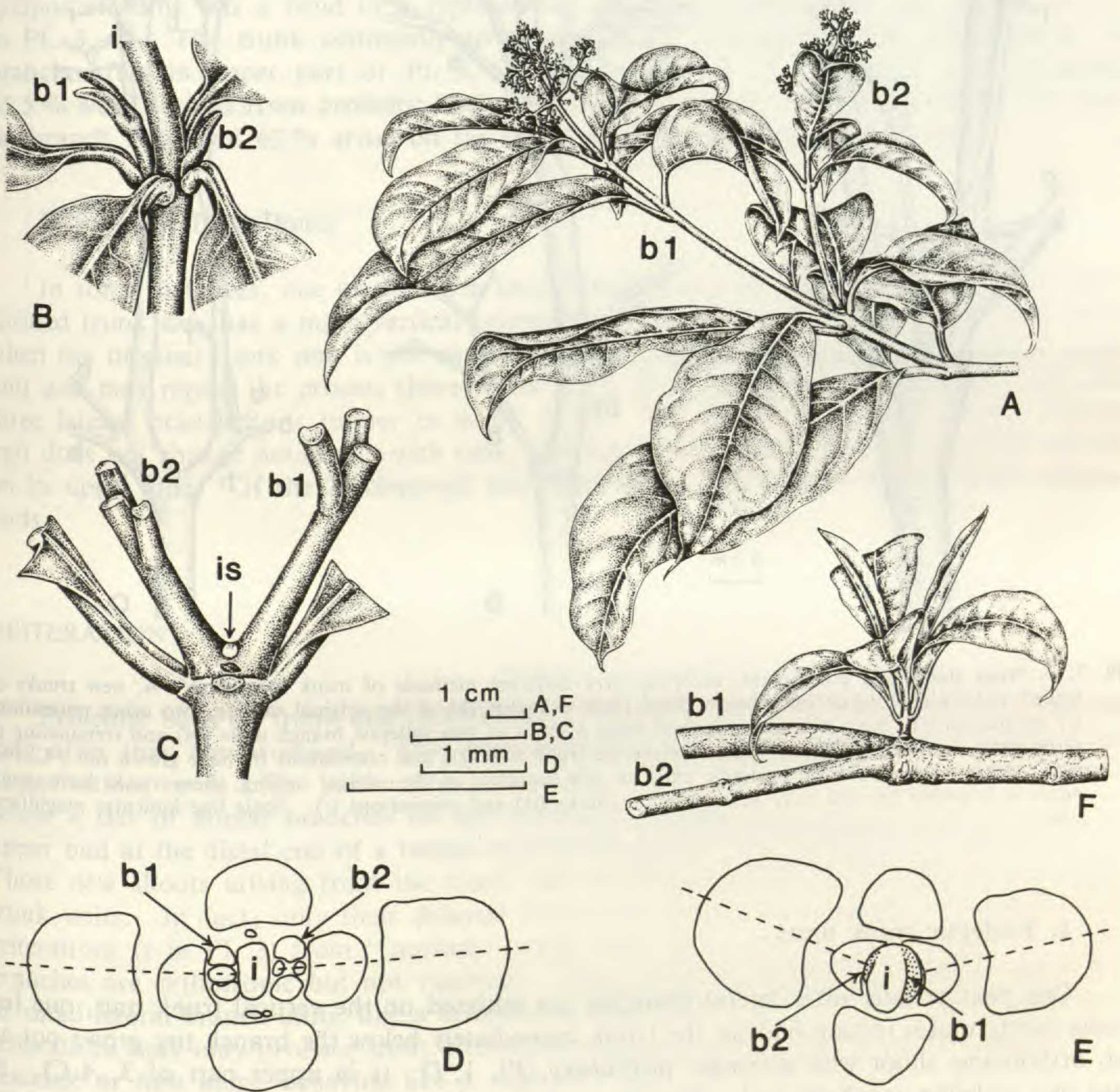
Pl. 2. — **Neea amplifolia** : **A**, branch units with dominant (b1) and subdominant (b2) flowering units from end of older unit ; **B**, end of old unit with terminal inflorescence (i) and growing branch units (b1, b2) ; **C**, end of older unit with inflorescence scar (is) and bases of mature branch units (b1, b2) ; **D**, apical bud of young branch unit after inflorescence (i) and new unit buds (b1, b2) formed, decussate phyllotaxy seen in this transverse section ; **E**, apical bud as in D but at younger stage, distorted decussate phyllotaxy seen in this transverse section. Scale lines indicate magnifications.
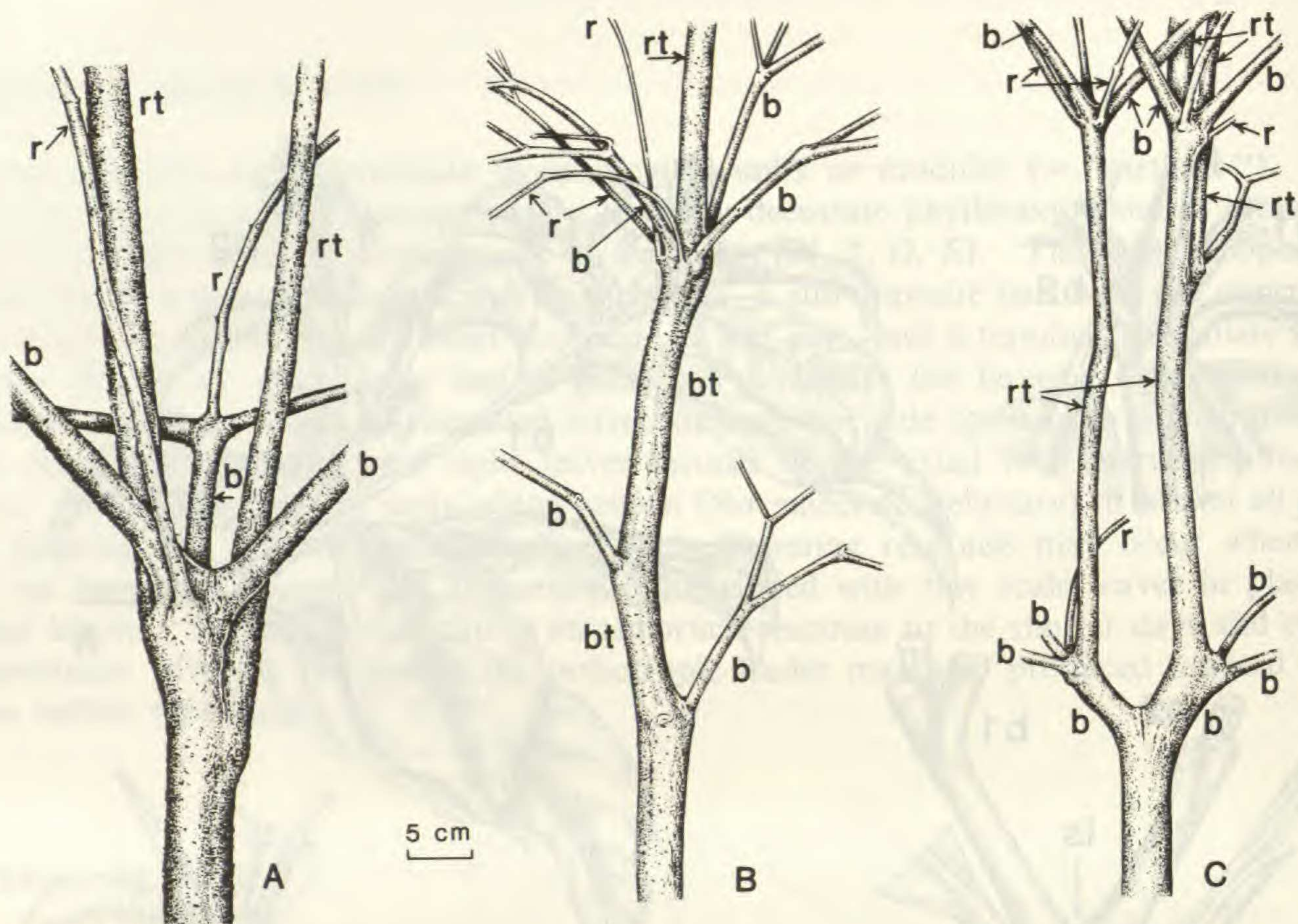
Pl. 3. — **Neea amplifolia**, older plants showing three different methods of trunk formation : **A**, new trunks or leaders (rt) from proleptic buds below distal three branches (b) of the original sapling, two other reiterations (r) are present ; **B**, base of a trunk derived from a series of two sylleptic branch units (bt) and terminating in three distal branches (b) below which a proleptic trunk unit (rt) and reiterations (r) have grown out ; **C**, two new trunks (rt) derived from proleptic buds on side branches of the original sapling, these trunks have terminated in branches (b) and have new proleptic trunks (rt) and reiterations (r). Scale line indicates magnification.

## 1. Proleptic trunk units

One year or later after lateral branches are initiated on the vertical trunk unit, one (or more rarely more) resting bud on the trunk immediately below the branch tier grows out as an orthotropic shoot with alternate phyllotaxy (Pl. 1, *D* ; rt in upper part of 3, *A-C*). It has two scalelike prophylls and often one or more additional reduced leaves before normal alternate and spirally arranged foliage leaves are produced. The shoot behaves like the original seedling axis and ends in an inflorescence and distal cluster or tier of lateral branch complexes. Out of 53 observed proleptic units (regardless of position of origin and including some reiterations), 34 % terminated in two branches and 66 % terminated in three branches. This proportion of the number of branches per tier is similar to that found in seedling axes. However, among those trunk units which terminated in three branches, 11 % had one or two sickly or soon aborting branches, thereby producing one or two functional lateral branches.

Another form of the proleptic trunk arises from a resting bud on the upper side of the distal end of a branch unit, usually the first unit at the base of the branch complex (rt in lower part of Pl. 3, C). The bud is next to the old inflorescence scar. In this case, the sympodial trunk has a bend in it representing the lateral branch unit (the two lowest b's in Pl. 3, C). The trunk commonly terminates in an inflorescence and distal cluster of branches (b's in upper part of Pl. 3, C). Of a total of 29 new trunk units observed, 65.5 % were derived from proleptic buds. Among these units, 37 % arose on the first lateral branch unit, and 63 % arose on the old trunk unit below the branch tier.

## 2. Sylleptic trunk units

In some instances, one of the three lateral branches at the end of the seedling or later-formed trunk axis has a more vertical orientation than its sister branches. This may occur when the original trunk unit is not exactly vertical. The branch then behaves like a trunk unit and may repeat the process (lower bt in Pl. 3, B) or terminates in an inflorescence and three lateral branch units (upper bt in Pl. 3, B). The orientation of the sylleptic branch unit does not change noticeably with time, although there is more secondary growth (wood) on its upper side. Of the 29 observed new trunk units, 34.5 % were derived from sylleptic buds.

## REITERATION

Proleptic buds on trunk and lateral branch axes in a variety of locations may grow out long after they are produced. This phenomenon occurs after injury to the leader, after decapitation, or in older parts of an intact tree. The activated buds tend to be directly below a tier of lateral branches on the orthotropic leaders (r in Pl. 3, A-C) or from the upper bud at the distal end of a lateral branch unit next to the inflorescence scar (Pl. 2, F). Those new shoots arising from the trunk axis are vigorous and behave like new proleptic trunk units. In fact, only their delayed outgrowth and greater numbers distinguish such reiterations (r in Pl. 3) from "normal" trunk units (rt in Pl. 3). Reiterations on lateral branches are orthotropic but not vigorous. They terminate in an inflorescence and a tier of small lateral branch units, like a deminutive trunk axis (r in Pl. 4, A). Sometimes, such reiterations may only produce short internodes and grow slowly without producing an inflorescence or new units, behaving like a vegetative short shoot (Pl. 2, F).

## GEOMETRY OF BRANCHING

The arrangement and orientation of all axes of the tree will be described, and averages (x̄) of observed values are given (n = number of observations, s = standard deviation). These values are used for computer simulations in the next section.

**10 cm**
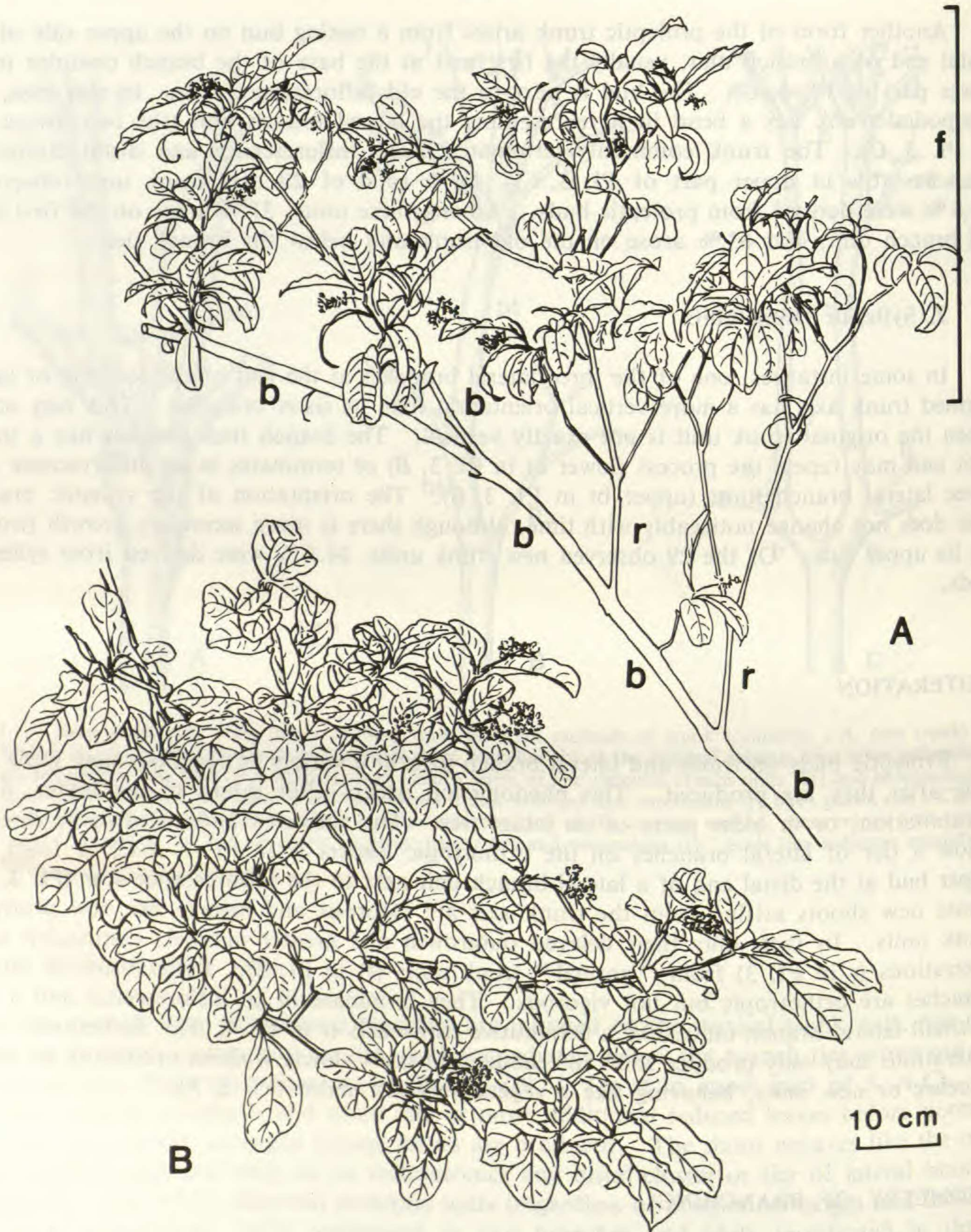
Pl. 4. — **Neea amplifolia**, parts of the canopy or crown in mature plants : **A**, base of lateral branch complex viewed from side, having a series of original branch units (b) and erect reiterations (r) which terminate in two or three lateral branches ; although the main lateral branch axis is oblique, the foliage layer (f) is essentially horizontal ; **B**, periphery of an old lateral branch at the base of the crown viewed from the side ; the main lateral branch axis bends down with new units bending upwards. Scale line indicates magnification.

The seedling axis or first trunk unit is radially symmetrical. Transverse sections of apical buds (Pl. 1, E) show that the average angle of divergence ($\alpha$) between successive leaves is 135.4° (n = 12, s = 9.199) which is very close to the theoretical divergence angle for a 3/8 phyllotactic spiral (= 135.0°). Because the genetic spiral (foliar helix) is compressed at the level of branching we could not directly measure $\alpha$ with certainty. We assumed that sequential buds developed into branches and, therefore, estimated $\alpha$. The average of the largest two of the three $\alpha$'s observed in branch tiers with three lateral branches (as in Pl. 1, A, F) is 133.1° (n = 22, s = 21.778). In tiers with only two laterals (as in Pl. 1, B), the largest of the two $\alpha$'s is 194.0° (n = 5, s = 10.246) which is 14° away from an opposite leaf arrangement (180°). This indicates a possible change in phyllotaxy below the terminal inflorescence from alternate to decussate.

The inclination with respect to gravity of the first units of lateral branches ($Inc_0$) is initially 22.8° (n = 9, s = 8.899) from vertical but increases with age until it stabilizes at 37.0° (n = 12, s = 6.901) after one year (see Pl. 5, A, B). However, the inclination of successive branch units ($Inc_1$, $Inc_2$) on the lateral branch complex becomes more horizontal with position away from the trunk (see Pl. 5, B, C). The inclination changes as shown in Table 1. The inclination of both units ($Inc_1$ and $Inc_2$) at the first bifurcation on a branch (N = 1) is essentially equal ($Inc_1 - Inc_2 \simeq 0$).

TABLE 1 : Inclination (Inc) of successive branch units in a lateral branch complex with respect to gravity. Mean ($\bar{x}$) in degrees, standard deviation (s), and sample size (n) are given. See Pl. 5 & 6, A for definitions of inclinations.

| | $Inc_0$ (First unit) | $Inc_1$ (Dominant unit, $R_1$) | | | | $Inc_2$ (Subdominant unit, $R_2$) | | | |
|---|---|---|---|---|---|---|---|---|---|
| Order (N) | 0 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| $\bar{x}$ | 37.0 | 52.9 | 61.8 | 73.8 | 73.4 | 60.2 | 50.8 | 58.0 | 50.6 |
| s | 6.90 | 13.32 | 17.08 | 7.77 | 8.83 | 6.70 | 14.56 | 13.42 | 12.43 |
| n | 12 | 10 | 12 | 7 | 11 | 4 | 6 | 7 | 9 |

| | $Inc_1 - Inc_2$ (Difference between daughter units) [a] | | | |
|---|---|---|---|---|
| Order (N) | 1 | 2 | 3 | 4 |
| $\bar{x}$ | 2.0 | 21.7 | 12.2 | 23.6 |
| s | 7.29 | 14.86 | 11.01 | 18.83 |
| n | 6 | 9 | 8 | 8 |

a. ($Inc_1 - Inc_2$) determined only from differences between paired values, therefore sample sizes are smaller than for $Inc_1$ and $Inc_2$ separately.

The extensions of these two initial branch units form the two main axes and establish the general plane of the branch complex. However, in successive bifurcations the inclination of $unit_1$ becomes more horizontal, until it is orientated at a stable 70° after the second order ($N \geq 3$). The data shown in Table 1 may seem contradictory at first viewing because of the different way data were collected for inclinations (upper part of Table) and differences (lower part of Table). Many individual branch units were pooled to get the average inclinations of a unit at a given order. Only paired new daughter units, those of the same bifurcation, were used to calculate the difference between new units and account for the discrepancies in absolute values. The differences in orientation between $unit_1$ and $unit_2$ ($Inc_1 - Inc_2$) ranges from 12.2 to 23.6°. $Unit_2$ is positioned out of the overall plane of the branch complex as the result of the non-horizontal plane of phyllotaxy (see Pl. 5, C; 6, A). This change in geometry is due to a positioning of $unit_2$ away from a position that is strictly opposite $unit_1$. In sectioned buds (Pl. 2, E) this change was 22.1° ($s = 14.264$, $n = 7$) ranging from 6 to 42°. Thus, the changes in $Inc_2$ are seen early in development and are not a result of later reorientation of the units. Taking into account the relatively large variances of the data in Table 1, we will approximate inclination values as given in the Appendix.

The bifurcation or branching angle of the new daughter units is defined as the angle between the mother and each new daughter unit ($\theta_1$ and $\theta_2$, respectively) measured in the most horizontal plane that includes the daughter unit (see Pl. 5, B, C). The sign of the angle indicates the relative direction, either left or right. Of the two new units, the dominant unit ($unit_1$) alternates its direction (see Pl. 6, C), and therefore its sign, with increasing orders of bifurcation (N). At the first bifurcation ($N = 1$), $|\theta_1| = |\theta_2| = 39°$. At higher orders ($N > 1$), $|\theta_1| < |\theta_2|$ although the total bifurcation angle ($|\theta_1| + |\theta_2|$) remains roughly constant as seen in Table 2.

TABLE 2 : Branching angles of daughter units in the lateral branch complex measured in the horizontal plane. Data given as : $\bar{x} \pm s$ (n) in degrees. See Pl. 5, B, C for definition of angles.

| Order (N) | $\theta_1$ | $\theta_2$ | $|\theta_1| + |\theta_2|$ |
|---|---|---|---|
| 1 | 39.2 ± 4.969 (5) | − 39.4 ± 4.505 (5) | 78.6 |
| 2 | 22.3 ± 9.539 (9) | − 41.5 ± 7.923 (9) | 63.8 |
| 3 | 25.1 ± 4.750 (6) | − 51.3 ± 14.541 (6) | 76.4 |
| ≥ 4 | 23.8 ± 4.810 (7) | − 46.5 ± 20.023 (7) | 70.3 |

With continued lateral branch growth each $unit_2$ also grows and flowers. However, more frequently only one new branch $unit_1$ develops instead of two new units. This single branch unit extends the old mother axis (which is a $unit_2$) in almost the same direction, i.e. $\theta_1 \simeq 0$, and a new $unit_2$ is less frequently produced on the old $unit_2$ mother. This aspect of a decrease in the frequency of branching is not dealt with in the later computer simulations because flow rates, which would approximate such changes, are not used.
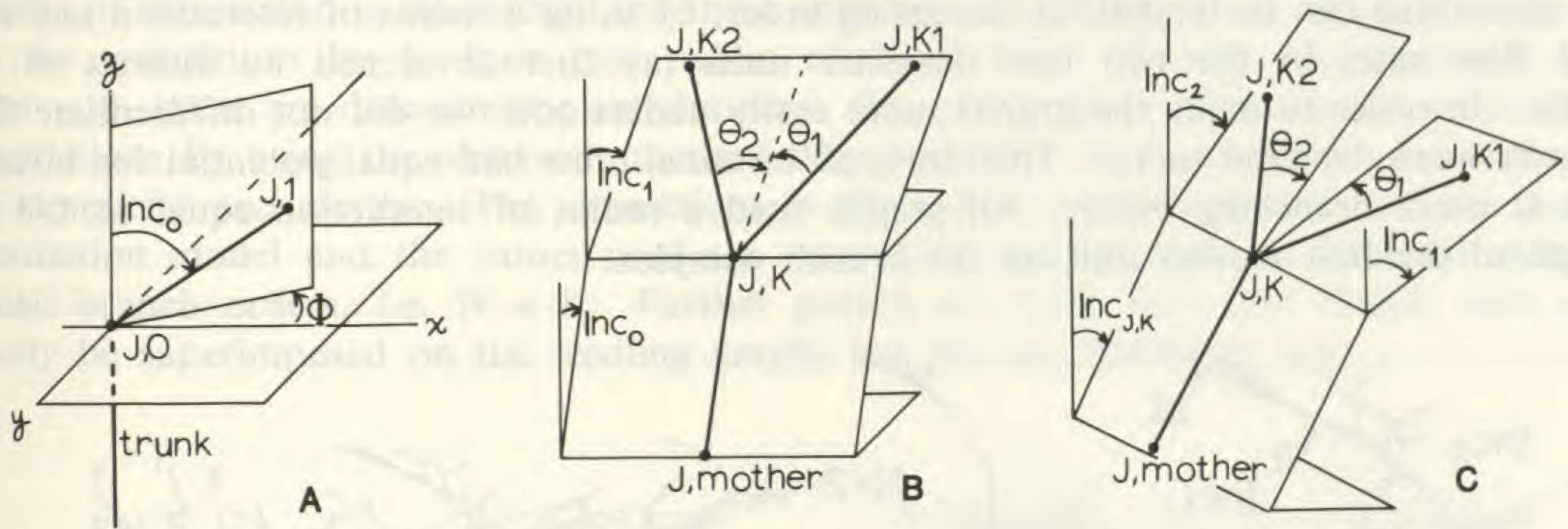
Pl. 5. — Diagrams of the geometry of branch units and of the parameters and symbols used in describing the position of the units : **A**, position of the first mother unit on the first branch of a tier ; $\Phi$ is a randomly selected angle in the xy-plane taken from the + x-axis ; $Inc_0$ is in a plane perpendicular to the xy-plane including the z-axis (= trunk) ; **B**, first bifurcation of a lateral branch (N = 1) in which $\theta_1 = \theta_2$ ; $Inc_0$ and $Inc_1$ are indicated ; **C**, later bifurcation of a lateral branch (N > 1) in which $\theta_1 \neq \theta_2$ and $Inc_1 \neq Inc_2$. See text (Pl. 6, *A, C*) and Appendix for further explaination.

The length of units within one branch complex tends to decrease with distance from the trunk. This shortening with increase in branch order is superimposed upon the differences in length between $unit_1$ and $unit_2$. However, the trend in unit lengths becomes obscured at N > 6 to 8 because a increasingly variable lengths. This loss of the regular geometric decrease in lengths found at smaller branch orders is presumably a result of greater phenotypic plasticity with branch order and hence age.

Reiterations also develop occasionally and grow vertically in harmony with the rest of the lateral branch complex such that the newly produced units and their foliage form a nearly horizontal layer of leaf surface which is continuous with the rest of the young, and therefore leafy, units of the units of the branch tier (f in Pl. 4, *A*). This effect can also be seen in simulated trees (Pl. 7, *A, C*). As units become older, their leaves abscise ; only the terminal two to three units bear leaves. The ends of old lateral branch complexes tend to bend downwards (Pl. 4, *B*). The younger leafy units grow upwards and compensate for their initial orientation, thereby displaying a plastic response common in many trees.

## COMPUTER SIMULATION AND THREE-DIMENSIONAL GRAPHICS

We ran a graphic simulation of the three-dimensional arrangement of the seedling axis and of the branch units of the first tier of lateral branches. The computer program is able to use means and standard deviations of the observed values to compute stochastic values for all parameters illustrated in Pl. 5. The parameter values, which are chosen to approximate observed values, and the details of the trigonometric equations are given in the Appendix.

Branching can be limited, at increasing order, by using a radius of interaction and unequal flow rates in the two new daughter units (as first developed by HONDA et al., 1982). In order to make the graphs more easily understood, we did not differentiate flow rates between daughter units. Therefore, all terminal units had equal potential for bifurcation at every branching order. All graphs used a radius of interaction equal to 1/3 the length of the first mother unit on the branch complex.
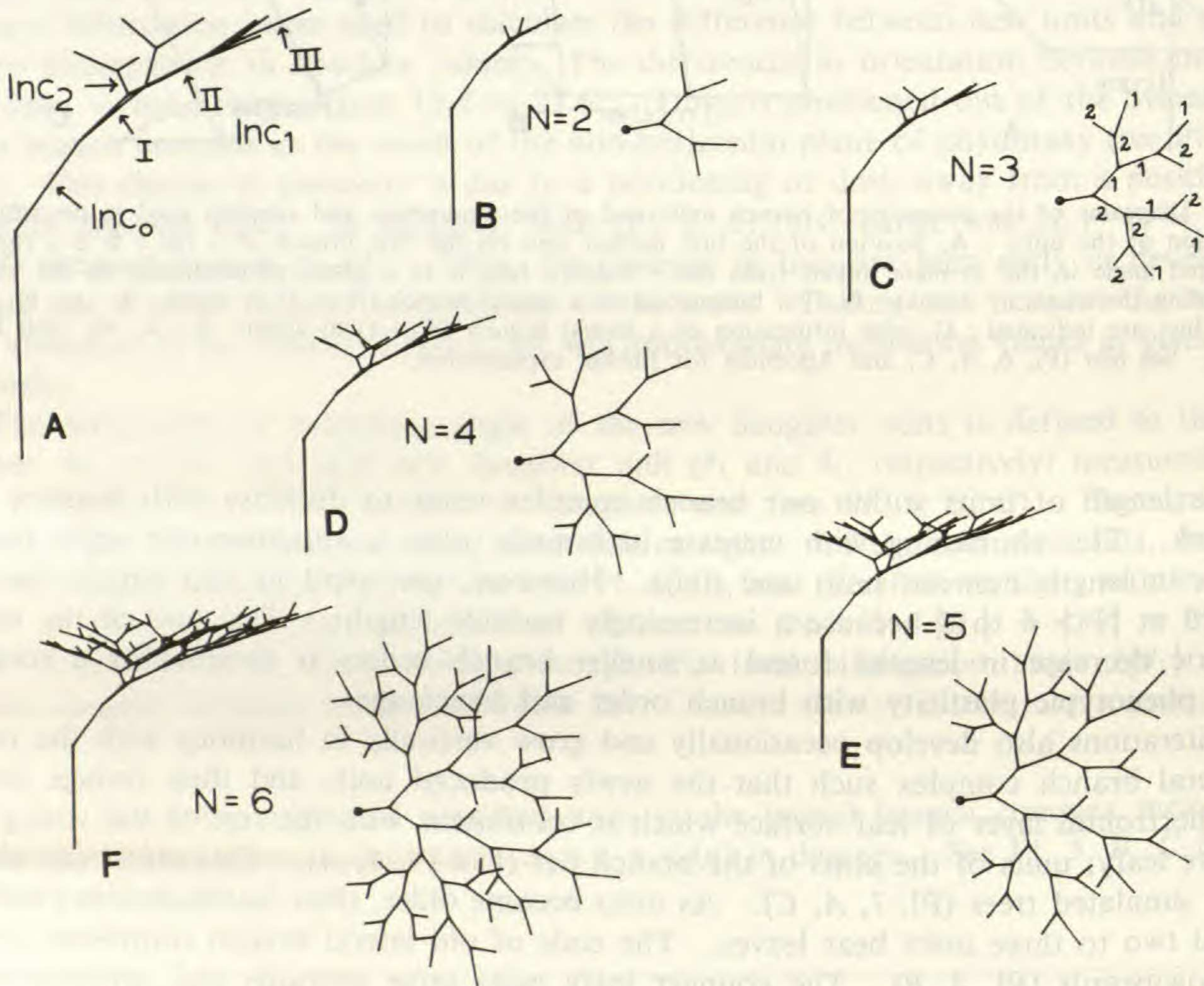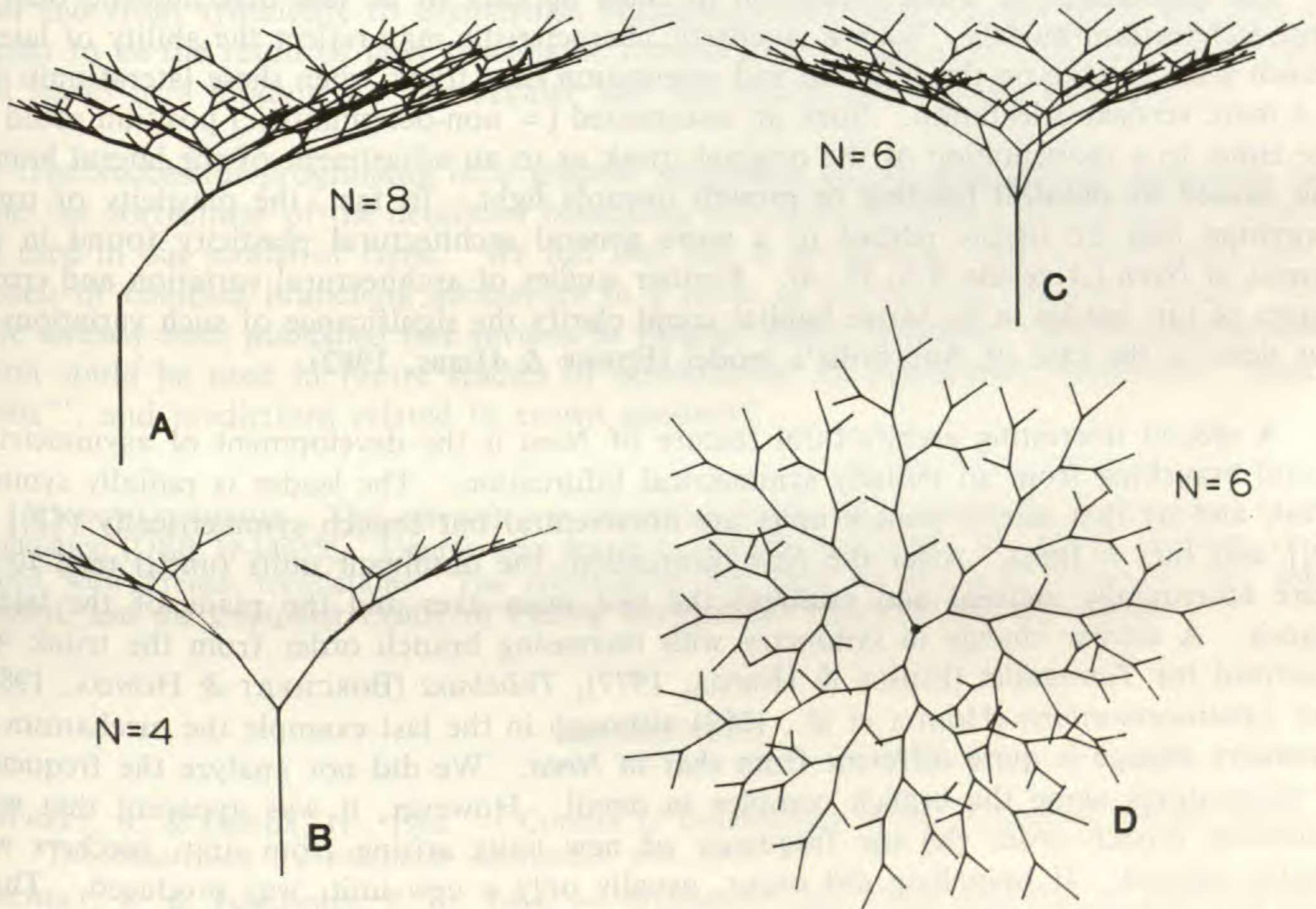


Pl. 6. — Graphic simulations of single branch complexes at the end of a vertical seedling trunk of **Neea** : A, branch after three bifurcations (N = 3) in side view ; inclinations of the first mother unit of the complex (Inc$_0$) and of the series (I, II, III) of dominant units (Inc$_1$) ; the inclination of unit$_2$ (Inc$_2$) at N = 2 is also indicated ; **B-F**, complexes with increasing bifurcation (N = 2 to 6) viewed from the side and from overhead ; the identities of unit$_1$ and unit$_2$ are shown in C.

A series of branch complexes is shown in Pl. 6, *B-F*. The complexes increase in branch order similar to a uniformly growing branch at discrete bifurcation intervals, which does not really occur in nature. The simulation does not account for terminal units which are still growing. In Pl. 6, *A* the changes in inclination from Inc$_0$ to Inc$_1$ (N = 1 to 3) are clear, as is the difference between Inc$_1$ (II) and Inc$_2$ at N = 2.

Views of tiers with two and three branch complexes are shown in Pl. 7. The overhead view of a tier may appear to have overlapping units (as in Pl. 6, *F* ; 7, *D*). In fact, the

radius of interaction is operating, and these units are at different levels which are separated in the z-direction by at least one radius of interaction. Because the standard deviation = 0, these are deterministic simulations. We can produce a population of stochastic simulations by using the observed standard deviations but chose not to do so for the sake of simplicity and clarity. The simulations in Pl. 6 & 7 are realistic and indicate that the simulation model and the values used are reasonable and accurate, at least for relatively small branch orders, i.e. N = 8. Further growth of trunk units and branch tiers could easily be superimposed on the seedling graphs but are not illustrated here.



Pl. 7. — Graphic simulations of a single branch complex and of branch tiers at the end of a vertical seedling trunk of **Neea** : **A**, complex after eight bifurcations (N = 8) in side view ; **B**, tier with two branch complexes at N = 4 in side view ; **C & D**, tier with three branch complexes at N = 6 viewed from the side and from overhead.

## DISCUSSION

Modular construction in *Neea* is well defined and regular, but a problem arises in interpreting the mechanism of height increment. One or more main trunk axes are regularly produced by either one of two methods : 1) from a fundamentally lateral, sylleptic branch unit ; or 2) from a resting, proleptic bud located either below the terminal ramification of

the preceeding trunk unit or on a lateral branch unit. The first method would place this species in Koriba's architectural model, and the second would place it in Prévost's model (according to HALLÉ et al., 1978). In addition, other new trunk units may later arise from proleptic buds on lateral branches. Since such trunks are usually small and not as vigorous as the sapling axis, they are interpreted as reiterations. However, the distinction between reiterations and the main trunk units in Prévost's model is a matter of the relative degree of vigour, as one of us (JBF) has observed in *Alstonia scholaris* (*Apocynaceae*), and thus remains subjective in the absence of more objective quantification.

The mechanism of trunk formation in *Neea* appears to be less deterministic than in most architectural models. Such a stochastic characteristic may reflect the ability of lateral branch units to take on the function and orientation of a trunk when these lateral units are in a more vertical orientation. Such an unexpected (= non-deterministic) position could be due either to a reorientation of the original trunk or to an adjustment of the lateral branch unit caused by physical bending or growth towards light. In fact, the plasticity of trunk formation may be simply related to a more general architectural plasticity found in the crowns of *Neea* (*A* versus *B* in Pl. 4). Further studies of architectural variation and crown shapes of this species in its native habitat could clarify the significance of such variations as was done in the case of Aubréville's model (FISHER & HIBBS, 1982).

A second interesting architectural feature of *Neea* is the development of asymmetrical lateral branching from an initially symmetrical bifurcation. The leader is radially symmetrical, and its first lateral branch units are dorsiventral but branch symmetrically ($|\theta_1| = |\theta_2|$ and $Inc_1 = Inc_2$). After the first bifurcation, the dominant units (unit$_1$) tend to be more horizontally inclined and establish the two main axes and the plane of the lateral branch. A similar change in symmetry with increasing branch order from the trunk was described for *Terminalia* (FISHER & HONDA, 1977), *Tabebuia* (BORCHERT & HONDA, 1984), and *Tabernaemontana* (HONDA et al., 1982) although in the last example the mechanism of symmetry change is quite different from that in *Neea*. We did not analyze the frequency of bifurcations along the branch complex in detail. However, it was apparent that with increasing branch order (N) the frequency of new units arising from unit$_2$ mothers was greatly reduced. If branching did occur, usually only a new unit$_1$ was produced. Thus, there is a reduction in branch numbers at higher orders as was found in other studies of branching pattern and geometry (BORCHERT & HONDA, 1984 ; BORCHERT & TOMLINSON, 1984 ; HONDA et al., 1981).

In *Neea* the subdominant units become more vertical and are positioned out of the general plane of the branch complex. In this way, the foliage layer of the lateral branch becomes thicker than in a more planar branch complex, e.g. *Terminalia* (FISHER & HONDA, 1979). Later reiterations from branch units, proceeding from the trunk to the periphery of a branch complex, grow in harmony so that the new leaves borne on these reiterations are maintained within a defined horizontal layer of foliage (f in Pl. 4, *A*). In the drooping, distal regions of large branches, the geometry is quite changed. New modules all bend upward to maintain the horizontal orientation of the foliage layer (Pl. 4, *B*). This would seem to be an opportunistic (= plastic) response to displacement of the lateral branch from

the horizontal. The distinction between opportunistic and deterministic patterns of growth and organization has been given by HALLÉ et al. (1978). The degree of environmentally induced plasticity, i.e. opportunistic architecture, was documented for Aubréville's model by FISHER & HIBBS (1982) and FISHER (in press). Only certain parameters of crown geometry appear to be plastic under differing light intensities, while others are strongly deterministic and constant.

The sections of young branch units show that the unequal inclination of the two daughter branch units is clearly established at or very soon after initiation of the unit buds and their subtending leaves (Pl. 2, *E*). Thus, the fundamental change from equal to unequal and from symmetric to asymmetric branching occurs early in ontogeny and does not appear to be the result of later twisting or reorientation of the axis. The number of nodes and leaves in a module are also regular and determined early in the bud.

The successful programing of a graphic simulation of the geometry of branching confirms the correctness of the details of branching rules and descriptive parameters of branching used in our model of *Neea*. We feel that this is yet another step in developing spatial models of complex branching geometries in a series of increasingly complex models which have already been published (see reviews in FISHER, 1984 ; in press). Such a graphic simulation could be used in future studies of optimization of parameters, theoretical "experiments", and predictions related to crown geometry.

## REFERENCES

BORCHERT, R. & HONDA, H., 1984. — Control of development in the bifurcating branch system of Tabebuia rosea : a computer simulation. *Bot. Gaz.* 145 : 184-195.

BORCHERT, R. & TOMLINSON, P. B., 1984. — Architecture and crown geometry in Tabebuia rosea (Bignoniaceae). *Amer. J. Bot.* 71 : 958-969.

DE CASTRO E SANTOS, A., 1980. — Essai de classification des arbres tropicaux selon leur capacité de réitération. *Biotropica* 12 : 194-197.

FISHER, J. B., 1984. — *Tree architecture : relationships between structure and function. In* WHITE, R. A. & DICKISON, W. C. (eds.), *Contemporary problems in plant anatomy*, pp. 541-589. Academic Press, Orlando.

FISHER, J. B., in press. — *Branching patterns and angles in trees. In* GIVNISH, T. J. (ed.), *On the economy of plant form and function.* Cambridge University Press, New York.

FISHER, J. B. & HIBBS, D. E., 1982. — Plasticity of tree architecture : specific and ecological variations found in Aubréville's model. *Amer. J. Bot.* 69 : 690-702.

FISHER, J. B. & HONDA, H., 1977. — Computer simulation of branching pattern and geometry in Terminalia (Combretaceae), a tropical tree. *Bot. Gaz.* 138 : 377-384.

FISHER, J. B. & HONDA, H., 1979. — Branch geometry and effective leaf area : a study of Terminalia-branching pattern. 2. Survey of real trees. *Amer. J. Bot.* 66 : 645-655.

HALLÉ, F., 1978. — *Architectural variation at the specific level in tropical trees. In* TOMLINSON, P. B. & ZIMMERMANN, M. H. (eds.), *Tropical trees as living systems*, pp. 209-221. Cambridge University Press, Cambridge.

HALLÉ, F. & OLDEMAN, R. A. A., 1970. — *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Masson, Paris, 178 p.

HALLÉ, F., OLDEMAN, R. A. A. & TOMLINSON, P. B., 1978. — Tropical trees and forests : an architectural analysis. Springer-Verlag, Berlin, 441 p.

HIBBS, D. E., 1981. — Leader growth and the architecture of three North American hemlocks. *Can. J. Bot.* 59 : 476-480.

HONDA, H., TOMLINSON, P. B. & FISHER, J. B., 1981. — Computer simulation of branch interaction and regulation by unequal flow rates in botanical trees. *Amer. J. Bot.* 68 : 569-585.

HONDA, H., TOMLINSON, P. B. & FISHER, J. B., 1982. — Two geometrical models of branching of botanical trees. *Ann. Bot.* 49 : 1-11.

REFFYE, P. DE, 1983. — Modèle mathématique aléatoire et simulation de la croissance et de l'architecture du caféier Robusta. IV. Programmation sur micro-ordinateur du tracé en trois dimensions de l'architecture d'un arbre. *Café, Cacao, Thé* 27 : 3-20.

## APPENDIX

### Simulations of branch geometry

The derivations of the space coordinates of the end points of all trunk and branch units are described below. The arrangement of the x, y and z-axes are given in Pl. 5, *A*. The inclination of the first unit of a lateral branch ($\theta_{oi}$) at the end of a trunk unit is also shown. The direction of the first branch unit is taken as a random angle ($\Phi$), thereafter sequential branches are ($= 135°$) apart, except for the case with only two branches per tier which are 180° apart. The first bifurcation of a branch (N = 1) is shown in Pl. 5, *B* in which $Inc_1 = Inc_2$. A later bifurcation (N > 1) is shown in Pl. 5, *C* & 6, *A* in which $Inc_1 > Inc_2$. Values for the parameters used in the simulations are indicated below and are either equal to or approximate the observed means.

First bifurcation : N = 1 (see Pl. 5, *B*)

Length ratios of daughter/mother unit : $R_1 = R_2 = 0.87$
Branching angles of daughter units : $\theta_1 = \theta_2 = 40°$
Inclination angles of daughter units : $Inc_1 = Inc_2 = 50°$

Length of mother unit = $Leng_m = [PX_{JK}^2 + PY_{JK}^2 + (PZ_{JK} - PZ_{mother})^2]^{1/2}$
$Inc_1 = Inc_2$
Length of daughter units : $Leng_1 = R_1 Leng_m$ ; $Leng_2 = R_2 Leng_m$

End points of daughter units :

$PX_{JK1} = PX_{JK} + [Leng_1 \sin (Inc_1) \cos (\Phi + \theta_1)]$
$PY_{JK1} = PY_{JK} + [Leng_1 \sin (Inc_1) \sin (\Phi + \theta_1)]$
$PZ_{JK1} = PZ_{JK} + [Leng_1 \cos (Inc_1) \cos (\theta_1)]$

$\left.\begin{array}{l} PX_{JK2} = \\ PY_{JK2} = \\ PZ_{JK2} = \end{array}\right\}$ as above but substitute : $Leng_2, \theta_2, Inc_2$

Later bifurcations : N > 1 (see Pl. 5, C & 6, A)

$R_1 = 0.95$, $R_2 = 0.76$ ; $|\theta_1| = 25°$, $|\theta_2| = 45°$ as measured in the most horizontal planes which include J, K and J, K1 and J, K and J, K2 ; respectively (Pl. 5, C).

Changes in the inclination :

when N = 2, $Inc_1 = 60°$, $Inc_2 = 50°$
when N ≥ 3, $Inc_1 = 70°$, $Inc_2 = 50°$

$U = PX_{JK} - PX_{mother}$
$V = PX_{JK} - PY_{mother}$
$W = PZ_{JK} - PZ_{mother}$

$$PX_{JK1} = PX_{JK} + \left[\left(\frac{R_1 \sin (Inc_1)}{\sin (Inc_{JK})}\right)\left(U\cos (\theta_1) - \frac{V (U^2 + V^2 + W^2)^{1/2}\sin (\theta_1)}{(U^2 + V^2)^{1/2}}\right)\right]$$

$$PY_{JK1} = PY_{JK} + \left[\left(\frac{R_1 \sin (Inc_1)}{\sin (Inc_{JK})}\right)\left(V\cos (\theta_1) + \frac{U (U^2 + V^2 + W^2)^{1/2}\sin (\theta_1)}{(U^2 + V^2)^{1/2}}\right)\right]$$

$$PZ_{JK1} = PZ_{JK} + R_1 (U^2 + V^2 + W^2)^{1/2}\cos (\theta_1) \cos (Inc_1)$$

$\left.\begin{matrix} PX_{JK2} = \\ PY_{JK2} = \\ PX_{JK2} = \end{matrix}\right\}$ as above but substitute $\theta_2$, $Inc_2$, and $R_2$

The computer program can use relative flow rates between the two daughter units and the mother unit and also can use the radius of interaction (both explained in HONDA et al., 1982) as a method to regulate the amount of branching within the branch complex. The frequency of bifurcations of both $unit_1$ and $unit_2$ are controlled in this way. For simplicity of presentation, the graphic simulations shown in Pl. 6 & 7 have flow rates of both $unit_1$ and $unit_2 = 1.0$ so that all units have the same potential to bifurcate at each branch order. However, branching was limited by the radius of interaction (the sphere of influence about the end points of pre-existing units which prevents a new unit from entering) equal to 1/3 the length of the first mother unit of the branch complex.